Helgoländer wiss. Meeresunters. 31, 285–297 (1978)

On the dynamics of exploited populations of *Tisbe holothuriae* (Copepoda, Harpacticoida)

VI. Response to perturbation by temporarily elevated mortality

M. Hoppenheit

Biologische Anstalt Helgoland (Laboratorium Sülldorf);
Wüstland 2, D-2000 Hamburg 55, Federal Republic of Germany

ABSTRACT: A total of 75 weekly exploited populations of the harpacticoid copepod *Tisbe holothuriae* Humes were exposed to 0.06, 0.3, 1.5, 7.5 or 37.5 μg $Cd^{++}l^{-1}$, combined with exploitation rates of 10, 30, 50, 70 or 90 % under conditions of surplus food supply at 22° C and 30 ‰ S. An unusually high mortality was observed for some weeks which could not be ascribed to the added amounts of Cd^{++}. A change in properties of supplied water is considered responsible for the unintentional perturbation which offered a further opportunity to study the effect of compensating reactions in stress situations. The results obtained clearly indicate an effect of exploitation rate on responses to detrimental influences. A superior performance has been found in populations exploited at higher rates. The findings are discussed with respect to earlier investigations on the population dynamics of *T. holothuriae*.

INTRODUCTION

To evaluate some of effects of different exploitation regimes on populations of the harpacticoid copepod *Tisbe holothuriae*, a number of experiments have been carried out in recent years regarding population density, age distribution, sex ratio, reproduction, growth and yield, as well as rate of development and survival time of the individual (Hoppenheit, 1975a, b; 1976). Some responses to lethal and sub-lethal exposure to cadmium have also been studied (Hoppenheit & Sperling, 1977; Hoppenheit, 1977). It has been reported that on the average only a few dead specimens were detectable in weekly samples because of cannibalism and rapid decomposition (Hoppenheit, 1975a; Hoppenheit & Sperling, 1977).

The present paper describes the first case where for some weeks high numbers of dead copepods were found. The experiments were performed to test the effects of low concentrations of cadmium (0.06 to 187.5 μg $Cd^{++}l^{-1}$) on population dynamics. Since other experiments conducted with much higher concentrations revealed no elevated numbers of dead specimens in weekly sampling (Hoppenheit & Sperling, 1977), the added amounts of Cd^{++} cannot be considered responsible for the high mortality observed in the present experiments. The unintentional temporary perturbation of the populations under examination offered a further chance to study the effect of compensating reactions in stress situations. The results obtained are discussed with respect to earlier findings.

MATERIAL AND METHODS

All the experiments reported here were designed in essentially the same manner as those described in previous publications of this series (Hoppenheit, 1975a, b, 1976; Hoppenheit & Sperling, 1977).

The populations of *Tisbe holothuriae* Humes were kept in 200 ml of non-aerated sea-water in 500-ml, wide-mouth, flat-bottom flasks at 22 ± 1° C in a room having 12h light per day. Fifteen populations each were exposed to 0.06, 0.3, 1.5, 7.5, 37.5 or 187.5 μg $Cd^{++}l^{-1}$. Subgroups of 3 replicates each were exploited weekly at rates of 10, 30, 50, 70 or 90 %. The specimens were fed dried mussel flesh (mantle, *Mytilus edulis)* once a week following exploitation. At the time of weekly harvests, 90 % of the contaminated medium was renewed. In samples of 10 ml taken before exploitation the numbers of nauplii and adults plus copepodids were determined. Vital staining with neutral red employed by Dressel et al. (1972) was used to distinguish between dead and live copepods.

RESULTS AND DISCUSSION

In a study on the effects of lethal concentrations of Cd^{++} on exploited populations of *Tisbe holothuriae* no significant increase in the fraction of dead specimens could be observed in weekly samples (Hoppenheit & Sperling, 1977). The low yield of dead individuals could be attributed to cannibalism and a high decomposition rate. An unusually high mortality at weekly sampling occurred in the present experiments where a total of 90 populations experienced sub-lethal concentrations of 0.06, 0.3, 1.5, 7.5, 37.5 or 187.5 μg $Cd^{++}l^{-1}$ at exploitation rates of 10, 30, 50, 70 or 90 %. For each combination of concentration and exploitation rate, three replicate populations were used in order to examine the extent of the expected poisonous effects of Cd^{++}.

In the course of these investigations the yield of dead specimens obtained following addition of Cd^{++} turned out to be independent of concentration. As no increased mortality could be detected at weekly sampling in populations exposed to lethal concentrations (Hoppenheit & Sperling, 1977), it has to be assumed that an external agent other than Cd^{++} accounted for the increase in mortality. As previous experiments suggested some relevant influence of the sea-water regularly transported to the laboratory (Hoppenheit, 1977), it is presumed that a fresh shipment of water used at the time when Cd^{++} was added to the culture solution induced the observed effect. Although precise information on the causes of the considered phenomena cannot be given, the findings are of some interest since they will, among other things, facilitate the answer to the question whether the reactions observed in diverse stress situations are similar or more or less specific to the detrimental influence.

The ratios of dead to live specimens obtained after the addition of Cd^{++} in Week 28 at 10, 50 and 90 % exploitation are plotted in Figure 1. Since no differences

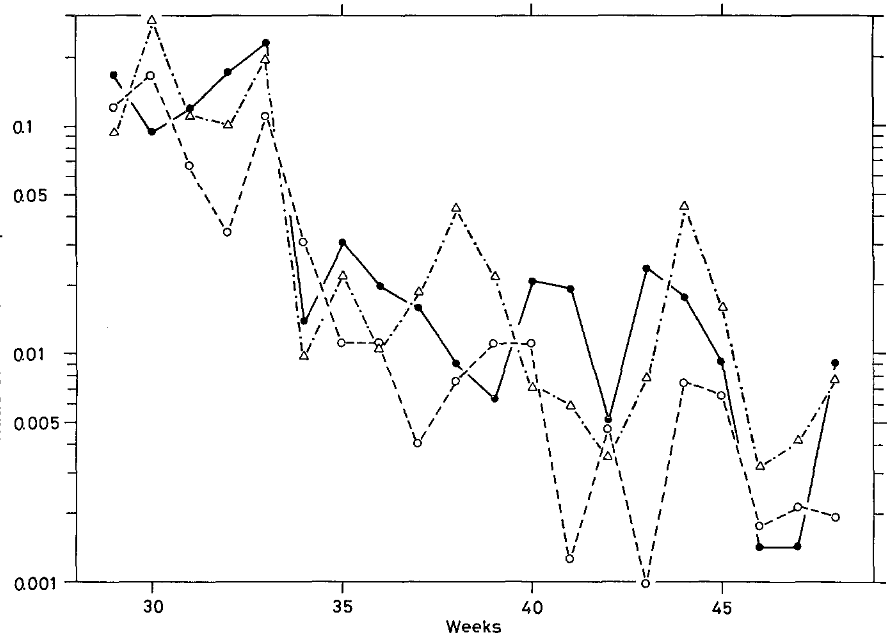

Fig. 1: *Tisbe holothuriae.* Detrimental influence of an assumed change in sea-water quality indicated by ratios of dead to live specimens. Each point represents the ratio of pooled data of 15 populations exploited weekly at rates of 10 (○), 50 (△) or 90 % (●). Addition of 0.06 to 37.5 μg Cd^{++}l^{-1} in Week 28 cannot be considered responsible for the effect observed

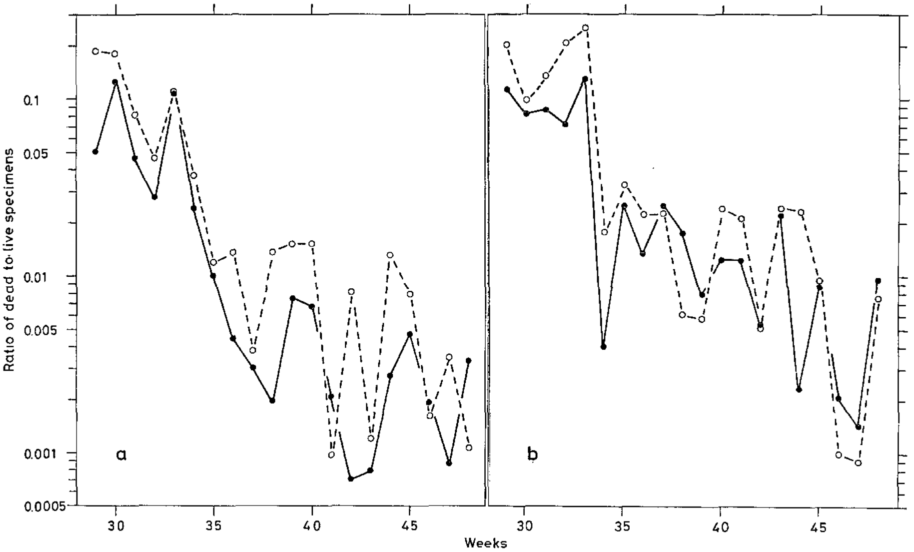

Fig. 2: *Tisbe holothuriae.* Detrimental influence of an assumed change in sea-water quality indicated by ratios of dead to live nauplii (○) and adults plus copepodids (●). Each point represents the ratio of pooled data of 15 populations exploited weekly at rates of 10 (a) or 90 % (b). Addition of 0.06 to 37.5 μg Cd^{++}l^{-1} in Week 28 cannot be considered responsible for the effect observed

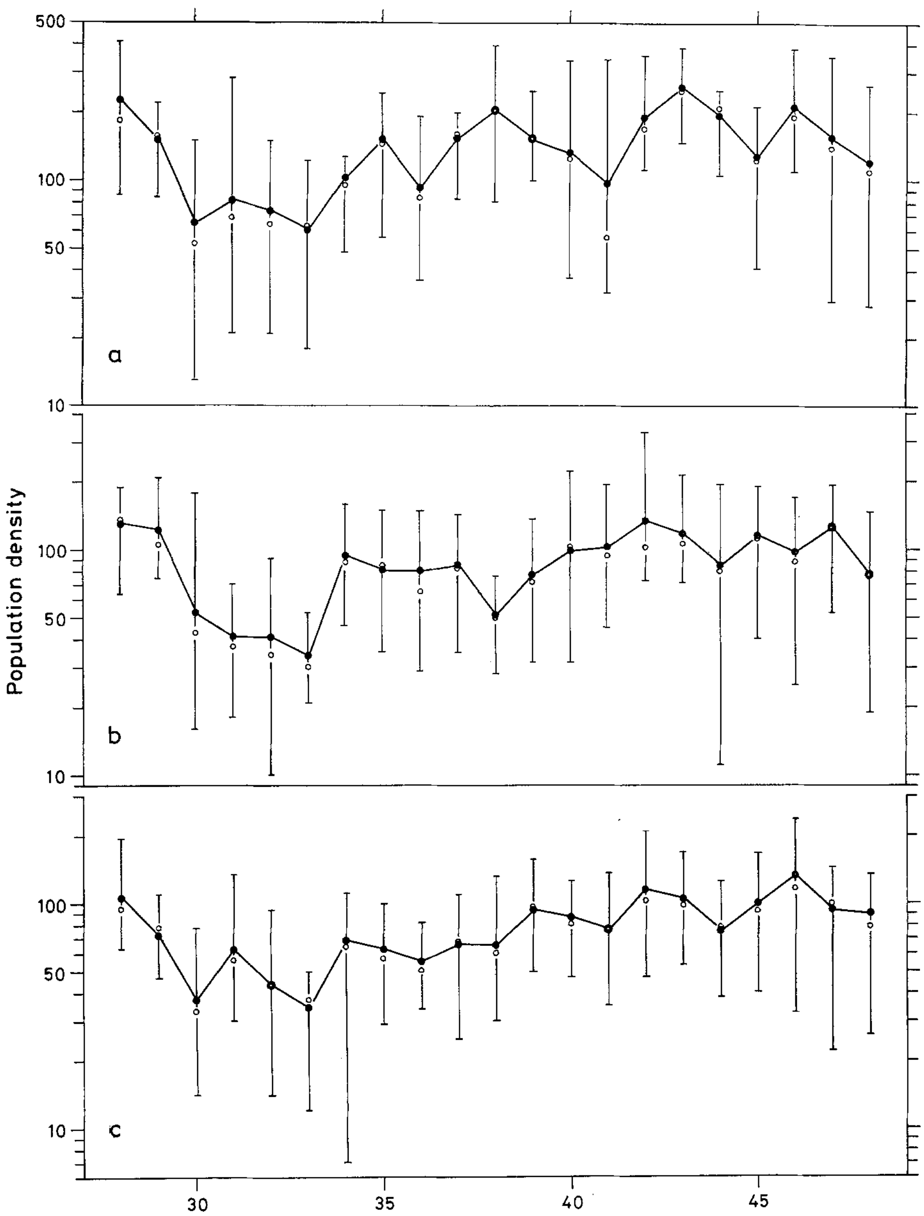

Fig. 3: *Tisbe holothuriae*. Variation of population densities before exploitation (number of specimens per 10 ml) in populations of adults plus copepodids exploited weekly at rates of 10 (a), 50 (b) or 90 % (c). Closed circles and bars represent mean and range of 15 populations. Medians are indicated by open circles

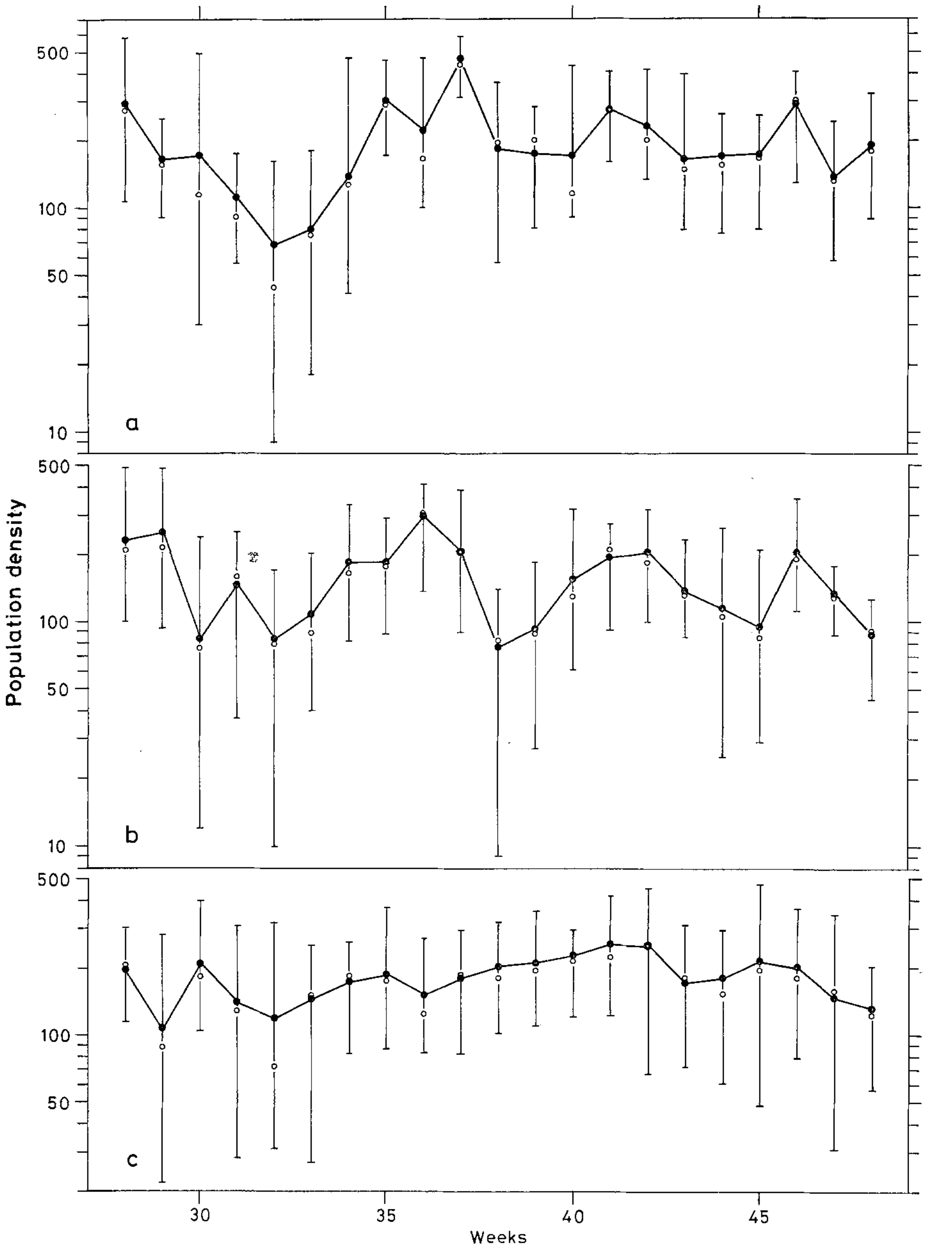

Fig. 4: *Tisbe holothuriae.* Variation of population densities before exploitation (number of specimens per 10 ml) in populations of nauplii exploited weekly at rates of 10 (a), 50 (b) or 90 % (c). Closed circles and bars represent mean and range of 15 populations. Medians are indicated by open circles

were found in the effects observed for the diverse concentrations of Cd^{++}, the data obtained from equal exploitation rates were pooled. Results gained at the concentration of 187.5 $\mu g\ Cd^{++}l^{-1}$ were not taken into account because it could be shown that this concentration temporarily reduces population size (Hoppenheit, 1977). Thus each point of Figure 1 represents the ratio of pooled data (totals of dead and live specimens) from 15 populations. The fraction of dead copepods was not determined before addition of Cd^{++}. The elevated mortality owing to the presumed but not identified change of sea-water quality lasted for five weeks, followed by a return to normal levels.

From the examples given in Figure 2 it can be seen that both the nauplii and adults plus copepodids suffered high death rates. In general, mortality has been found to be higher among nauplii than among adults and copepodids (cf. Hoppenheit, 1976).

Variation of population densities in the populations of adults plus copepodids is demonstrated in Figure 3. At each exploitation rate (results at 30 and 70 % exploitation are not shown) the mean population density exhibits a significant U-shaped trend (proven by Ofenheimer's test, 1973) at the beginning of the experimental period. In the majority of cases the medians (open circles) are smaller than the means (closed circles), indicating positive skewness of the population density distributions.

The responses of the populations of nauplii to the assumed change in water properties are given in Figure 4. Again the significances of the U-shaped trends were proven by the Ofenheimer test (1973). A significance level of $\alpha < 0.005$ was obtained at 10 and 30 % exploitation, at 50% exploitation $\alpha < 0.05$ resulted and no significant trends could be established at the other two rates ($\alpha > 0.10$). In contrast to the minima, the maxima of the values obtained show little variation at 70 and 90 % exploitation. The compensatory reaction to the decrease in population density in populations exploited at rates of 10, 30 or 50 % led to an overshoot in density during Weeks 36 and 37, respectively.

Immediately after the addition of Cd^{++} in Week 28 the relative frequencies of nauplii started to rise significantly in populations exploited at rates of 70 or 90 % (Fig. 5). In populations exploited at lower rates the increase of relative frequencies of nauplii was delayed.

All populations were exposed to Cd^{++} for 30 weeks (results from only 20 weeks are shown here) after which the populations experiencing 0.06, 1.5 or 37.5 $\mu g\ Cd^{++}l^{-1}$ were supplied with Cd-free water for 22 weeks. After this period they were again exposed to Cd^{++} (same concentrations as before) and observed for a further 17 weeks. No elevated mortality could be established during the second period of Cd^{++} administration.

The results of the present paper clearly indicate that the exploitation rate has an effect on the influence of detrimental environmental factors. From the variation in population densities as a function of time (Hoppenheit, 1977; Fig. 1, p. 505) it was concluded that no relationship between magnitude of the effect observed following Cd^{++} administration (148 $\mu g\ l^{-1}$) and exploitation rate exists. From further calculations it appeared that the reduction found in population density after the addition of 148 or 222 $\mu g\ Cd^{++}l^{-1}$ was less at higher exploitation rates. Figure 6 of the present paper shows the smoothed curves of the mean densities of 6 pooled populations each of

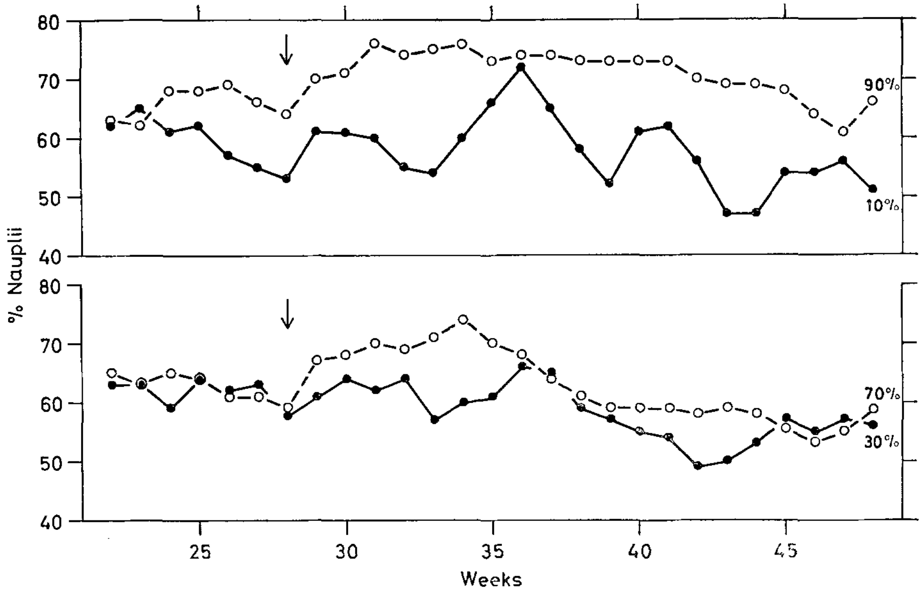

Fig. 5: *Tisbe holothuriae.* Variation of relative frequencies of nauplii in populations exploited at rates of 10, 30, 70 or 90 %. Each point represents the mean of 15 populations. Change in experimental conditions (assumed change in sea-water quality) is indicated by an arrow

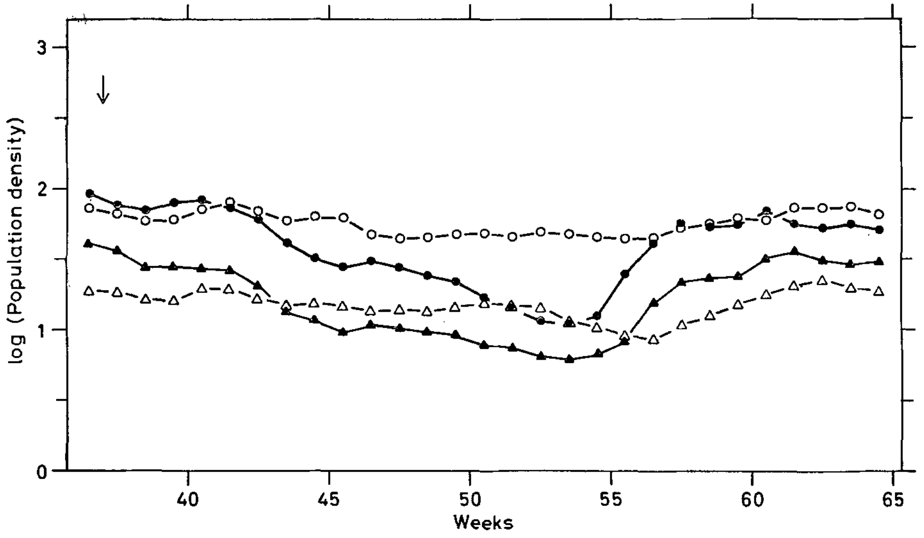

Fig 6: *Tisbe holothuriae.* Variation of mean densities before exploitation (number of specimens per 10 ml, moving average of 6 items) of pooled populations of nauplii (●, ○) and adults plus copepodids (▲, △) exploited weekly at rates of 10 (●, ▲) or 90 % (○, △) after the addition of 148 or 222 μg $Cd^{++}l^{-1}$ (indicated by an arrow). Each point represents mean of 6 populations

nauplii and adults plus copepodids, exploited at rates of 10 and 90 %, respectively, and exposed to 148 or 222 μg $Cd^{++}l^{-1}$ (cf. Hoppenheit, 1977). As no control experiments were performed at the exploitation rate of 90 %, comparisons cannot be made between affected and unaffected density trends at this rate as was undertaken for populations exposed to 10 % exploitation (cf. Hoppenheit, 1977). The results are in concordance with the present findings of a more shallow response in populations exploited at higher rates.

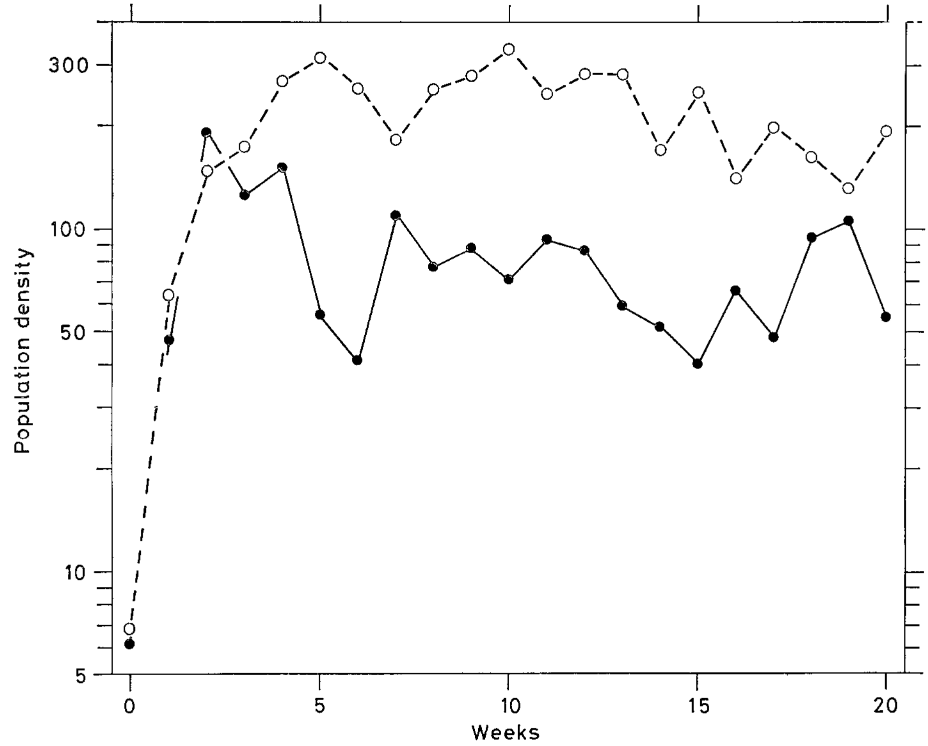

Fig. 7: *Tisbe holothuriae.* Variation of population density before exploitation (number of specimens per 10 ml) in populations exploited at rates of 10 (●) or 70 % (○). Points represent means of 5 Populations

The superior performance of the populations exploited at higher rates may be attributed to different mechanisms. As mean population density between exploitations is inversely related to the degree of exploitation (cf. Hoppenheit, 1976), deleterious effects of crowding are less severe at higher removal rates. Improved "well-being" and consequently higher physiological flexibility of individuals (cf. Slobodkin, 1968) at 70 or 90 % exploitation may therefore result in less intense responses.

Some indication for assuming an improved "well-being" at higher exploitation rates is given by the inverse relation of adults' size to mean population density between exploitations (cf. Hoppenheit, 1976). Although food was offered in surplus, the increased competition at higher mean population densities seems to have reduced food intake per individual. Figure 7 gives the time curves of mean population densities before weekly exploitation, for 5 populations each exploited at rates of 10 and 70 %, respectively. Figure 8 shows the corresponding mean lengths of adult females (measured without furcal setae); the population flushes led to markedly reduced sizes in the females. As length of copepod females are positively correlated with number of eggs carried in the egg sac (cf. Marshall, 1949; Ravera & Tonolli, 1956; McLaren, 1965; Smyly, 1968; Rippingale & Hodgkin, 1974; Zurlini et al. 1978), more eggs per egg sac are consequently produced at higher exploitation rates (cf. Hoppenheit, 1976).

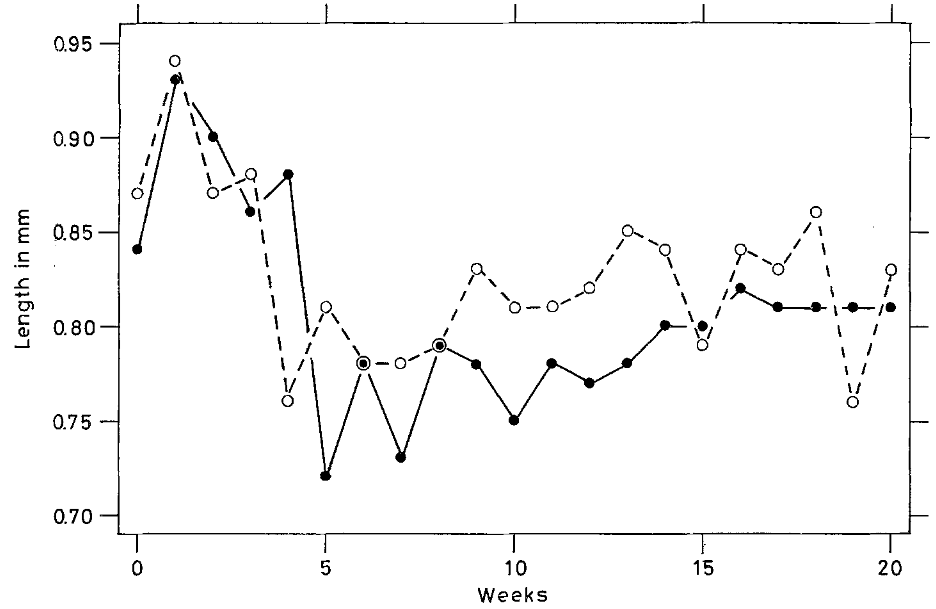

Fig. 8: *Tisbe holothuriae.* Variation of mean length of adult females of 5 pooled populations each exploited at rates of 10 (●) or 70 % (○). Each point represents mean of 3 to 47 measurements. Standard deviation: 0.03 to 0.08

The ability of populations of *Tisbe holothuriae* to adapt to unfavourable conditions of life in small volumes of water may be taken as an indication of high genetic variation. An adaptation of the gene pool to conditions produced by the different exploitation rates should therefore be taken into account.

Harpacticoid copepods appear to be typical r-strategists with rapid development and high reproductive potential (cf. Heip, 1974). The present experiments indicate that the reduced effect of crowding by increased relative mortality and consequently lowered population size does not bring about an immediate change of the population structure in favour of the nauplii in populations exposed to 10 or 30 % exploitation, as is the case in populations exposed to higher rates (cf. Fig. 5). It may therefore be concluded that the positions of the populations exploited at lower rates and which steadily exist around their equilibrium levels shift along the r-K continuum in favour of a K-strategy. Before the appearance of increased mortality the populations were maintained under constant exploitation for 28 weeks. Since generation time was established to be 7.9 days at 22° C (Hoppenheit, 1976), this period corresponds to 25 generations.

In earlier experiments (Hoppenheit, 1976) it was found that on the average less eggs per egg sac were produced at lower removal rates or higher densities between exploitations. Embryonic death rate and mortality in nauplii were both raised in populations exploited at lower rates and more rapid embryonic development could be established at higher rates of exploitation. The high selective pressure under crowded conditions might have the effect of selecting in favour of low reproductive rate to such an extent that the populations are unable to increase reproductive performance immediately when an elevated mortality occurs (cf. Fig. 5). The response is delayed and leads to an overshoot in population density as well as fraction of nauplii about 8 weeks (7 generations) following the appearance of high numbers of dead individuals. The question is whether or not the observed periods of time are sufficient for an adaptation to lowered population density and re-adaptation to crowded conditions as experienced in the selection history prior to the perturbation.

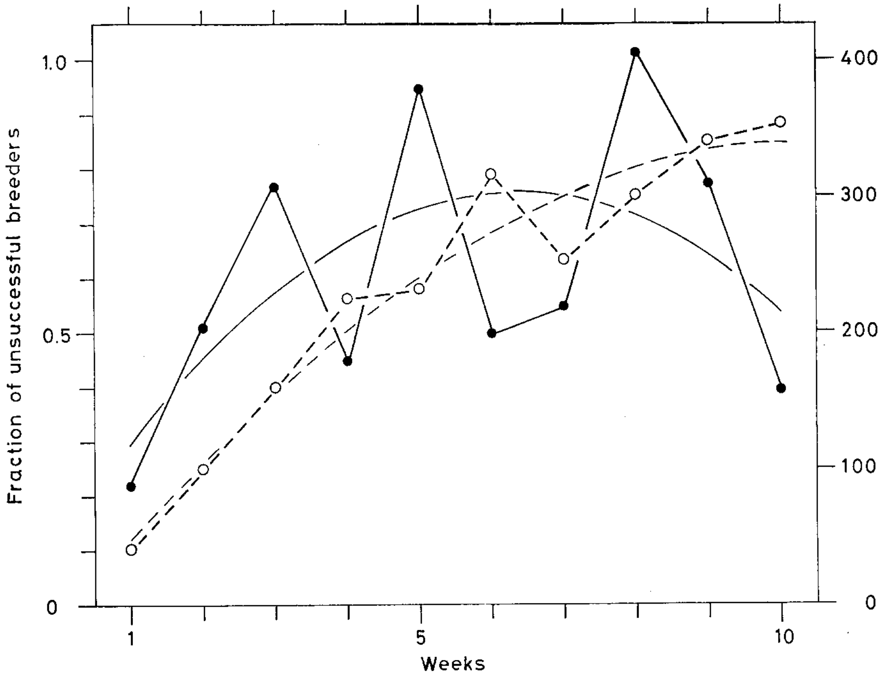

Fig. 9: *Tisbe holothuriae*. Variation in population density (number of specimens per 10 ml) (●) and fraction of unsuccessful breeders (○) in a population exploited weekly at a rate of 10 %. Trends are given by second degree polynomials

Populations exploited at rates of 70 or 90 % and consequently exposed to lower selective pressure and relatively higher variability of the environment in regard to population density appear to carry a higher degree of genetic variability indicated by an increased dispersion of data in numbers of eggs, nauplii and adults produced per egg sac (cf. Hoppenheit, 1977; Figs. 7–9). This may allow a faster and more efficient response to elevated mortality.

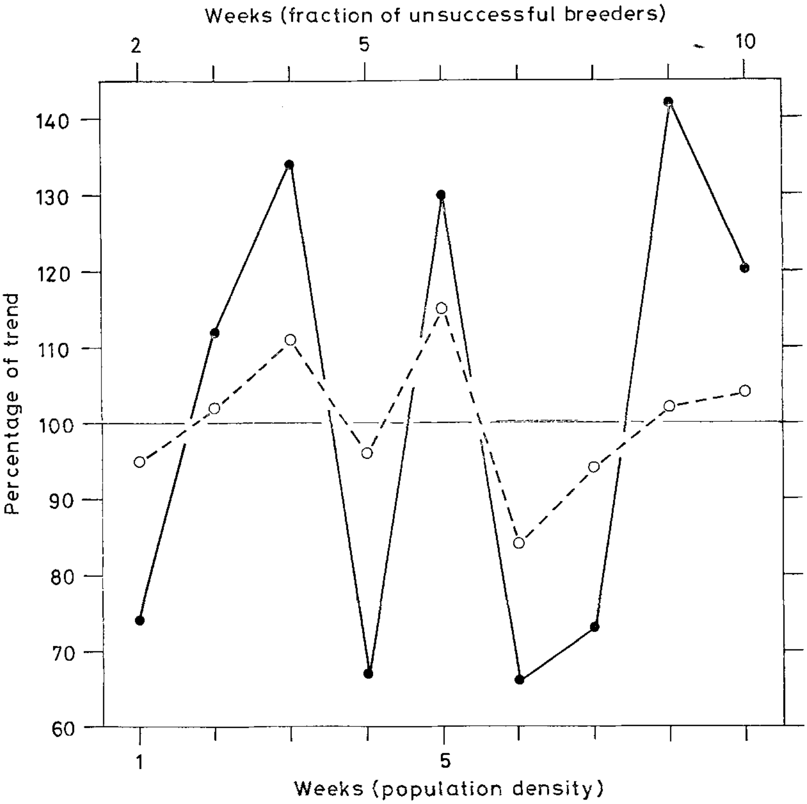

Fig. 10: *Tisbe holothuriae.* Percentages of trends in population density (●) and fraction of unsuccessful breeders (○) in a population exploited weekly at a rate of 10 %

Some preliminary experiments conducted with populations exploited at rates of 10 % for 17 weeks (ca. 15 generations) indicated that the populations are able to react readily with an increase of the naupliar fraction when the rate is changed to 50 or 90 % exploitation. Assuming the relatively short period of 17 weeks before change in exploitation rate was in fact long enough to allow some changes in gene frequencies, it may be argued that adaptation to crowding alone cannot be responsible for the delayed response described above.

A further point requires consideration: As reported in a preceding paper (Hoppenheit, 1976; cf. Fig. 4), isolated females originating from populations exploited at a rate of 90 % revealed an accelerated egg sac formation frequency shortly after isolation. The possibility of an "environmentally-cued polymorphism" (cf. Clark, 1976) producing morphs congruent with conditions given by the exploitation regime must therefore be taken into account.

It has further been reported (Hoppenheit, 1976; 1977) that the fraction of egg sacs from which no adults arise depends on exploitation rate or mean population density between exploitations. From Figure 9 (Hoppenheit, 1977) it can be seen that differences in the mean production of adults per egg sac at different exploitation rates are mainly caused by the fraction of unsuccessful breeding individuals. Further, if population density falls short of a certain value, the age structure shifts in favour of the nauplii (Hoppenheit, 1977). These findings may be taken as an indication of a dynamic strategy in *Tisbe holothuriae* switching between relative r- and relative K-positions along the r-K continuum. In populations of such strategists, changes in reproductive activity are cued by environmental conditions and occur within the same individuals (cf. Nichols et al., 1976).

In Figure 9 the time curves of population density and fraction of egg sacs from which no adults arise at the exploitation rate of 10 % are shown. The description of trends by second-degree polynomials and calculation of percentages of the quadratic regressions yielded the plots of Figure 10: the population density is positively correlated with the fraction of unsuccessful breeders with a time lag of 1 week ($r = 0.83$). Thus if population density is below its trend line, the fraction of unsuccessful breeders moves in the same direction one week later. Fluctuations of the two time series in populations exploited at 90 % show the same dependency.

As stock populations were reared in the laboratory for several years before onset of the experiments described and the populations exposed to the higher exploitation rates also experienced strong crowding (independent of the removal rate the populations reach approximately the same biomass prior to next exploitation), it must be taken into consideration that in the present case a dynamic strategy could be the result of an adaption to the specific rearing conditions, with exploitation being of secondary importance.

Possibly all mechanisms discussed act together in compensating for detrimental effects as described by Slobodkin (1968) in completeness of detail.

Acknowledgements. The author thanks Mrs. H. Rade, Mrs. K. Bote and Mrs. I. Ziehr for their assistance in the experiments, Mrs. E. Zimmermann and Dr. C. N. Murray for help in preparation of the manuscript as well as Miss R. Kleinfeld for drawing the figures.

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